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Elastic Net Model of Ocular Dominance: Overall Stripe Pattern and Monocular Deprivation

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Abstract

The elastic net [Durbin & Willshaw 1987] can account for the development of both topography and ocular dominance in the mapping from the lateral geniculate nucleus to primary visual cortex [Goodhill & Willshaw 1990]. Here it is further shown for this model that (a) the overall pattern of stripes produced is strongly influenced by the shape of the cortex: in particular stripes with a global order similar to that seen biologically can be produced under appropriate conditions, and (b) the observed changes in stripe width associated with monocular deprivation are reproduced in the model.

1 Introduction

Two well-documented phenomena associated with ocular dominance stripe formation in primary visual cortex are as follows. Firstly, for the macaque monkey there is a global order to the stripe pattern [LeVay et al 1985]. Secondly, the relative widths of left- and right-eye stripes can change following monocular deprivation in the cat [Shatz & Stryker 1978] and in the macaque [Hubel et al 1977]. In this short paper empirical results are presented for the elastic net model of ocular dominance, showing that it can reproduce both these phenomena under appropriate conditions.

The elastic net is an algorithm for finding neighbourhood-preserving mappings between spaces of different dimensionalities [Durbin & Willshaw 1987]. It was originally developed from a model for retinotopic map formation [Willshaw & von der Malsburg 1979], and has been applied to the problem of finding mappings that are both striped and topographic, such as the ocular dominance map [Goodhill & Willshaw 1990]. The algorithm finds a mapping between a "feature" space and a "cortical" space. For the topography and ocular dominance problem, the feature space consists of all positions in both eyes, and here we refer to these feature points as LGN (lateral geniculate nucleus) units. Distances between LGN units in the space encode the "similarity" of units to each other, such that similar units lie close to each other. Similarity could be interpreted as the degree to which the activity of units is correlated in the feature space [Yuille et al 1991]. Each LGN is represented as a two-dimensional sheet of points, and the two sheets lie atop one another separated by a small gap. The third dimension represents ocularity: distances in the ocularity dimension represent similarities according to the same metric as in the other two dimensions. The images of cortical points under the mapping are envisaged as an elastic sheet moving in the feature space: these points are referred to as cortical units. For a fuller discussion of this formulation of the problem see [Goodhill 1991].

Refer to the positions of LGN units as x_i and cortical units as y_j. The change in the position Δy_j of each

cortical unit at each time step is given by

$$\Delta y_j = \alpha \sum_i w_{ij}(x_i - y_j) + \beta k \sum_{j' \in N(j)} (y_{j'} - y_j) \tag{1}$$

The first term is a matching term that represents the "pull" of LGN units for cortical units, which is traded off with ratio $\alpha/\beta k$ against a regularization term representing a "tension" in the sheet, i.e. a desire for neighbouring cortical units to represent neighbouring points in the feature space. $N(j)$ refers to the set of points in the sheet that are neighbouring to j. The "weights" w_{ij} are defined as follows:

$$w_{ij} = \frac{\Phi(|x_i - y_j|, k)}{\sum_p \Phi(|x_i - y_p|, k)} \tag{2}$$

where

$$\Phi(|x_i - y_j|, k) = \exp\left(\frac{-|x_i - y_j|^2}{2k^2}\right) \tag{3}$$

Over the course of a simulation, the scale parameter k is gradually reduced, so that the matching term comes to dominate the regularization term.

These equations can be interpreted as saying that each cortical unit has a gaussian receptive field at position y_j in the feature space [Durbin & Mitchison 1990]. The amount by which cortical unit j responds to input i at position x_i is given by w_{ij}. The normalization of w_{ij} by the response of all other cortical units to input i implements a form of soft competition between cortical units. Although all cortical units are adapted towards input i, those that respond most strongly are adapted the most. The first term can therefore be seen as Hebbian. The second term says that cortical units are also adapted towards inputs that their neighbours respond to.

It was shown in [Goodhill & Willshaw 1990] that stripe width is controlled by the ratio of the separation of corresponding units between the LGN sheets to the separation of neighbouring units within each LGN sheet. A simple analysis in one dimension suggests that stripe width increases linearly with this ratio [Goodhill 1991]. A much deeper analysis of stripe width in the elastic net model can be found in [Dayan 1993], where the relative influences of the input similarities and the cortical interaction function are determined. Interpreting similarity as correlation, stripe width for the elastic net *increases* as the degree of correlation between the two eyes *decreases*. Similar behaviour is found in the competitive model of [Goodhill 1993], where the prediction was made that stripe width should thus be wider in strabismatic cats than normal cats. This prediction has recently been confirmed experimentally [Löwel & Singer 1993].

2 Overall stripe pattern

Naturally occuring ocular dominance stripes in the monkey exhibit global order: stripes remain roughly parallel over large distances along the dorsal-ventral axis. This result might not be expected from the operation of the purely local mechanisms that are present in most models. [LeVay et al 1985] provide a review of theoretical ideas regarding possible sources of an anistropic ordering influence, and hence how such global order might arise. Such ideas include elongation of geniculocortical arborizations [von der Malsburg 1979], anisotropic growth of the cortex [Swindale 1980], and differences in the strength of two orthogonal gradients of adhesiveness [Fraser 1985]. [LeVay et al 1985] suggest that the effect could be due to the *shape* of primary visual cortex as compared to the shape of the LGNs. The basic geometry of the mapping in the macaque is that of two roughly circular LGN layers projecting to a roughly elliptical region with a ratio of major to minor axes of 2:1. Assume that the map is interdigitated into parallel stripes. Then, in order to fit both of the circular LGN regions into the elliptical region, each circular region will be less "stretched" if stripes are formed running parallel to the short axis of the ellipse, compared to the case of stripes running

parallel to the long axis. This hypothesis was tested for the elastic net algorithm by comparing the mapping formed between two disks of LGN units and a sheet of cortical units that is (a) a disk and (b) an elliptical region as described above. The dimensions of the cortex were chosen such that the number of units was about the same as the total in both LGNs. Results are shown in figure 1. It can be seen that the shape of the cortex exerts a strong influence on the overall stripe pattern: for a circular boundary there is no preferred stripe orientation, whereas for an elliptical boundary stripes are indeed aligned with the short axis, as seen biologically.

This boundary effect could in general provide another test of the adequacy of models for ocular dominance, for instance [Miller et al 1989, Obermayer et al 1992]. It would not be expected to occur in models where there is no consideration of topography (such as [Swindale 1980]), since the effect relies on the undesirability of stretching, i.e. deformations in topography in certain directions. The cortical shape effect hypothesised by [LeVay et al 1985] has also recently been demonstrated in a different computational scheme by [Jones et al 1991]. They defined a particular cost function measuring topographic distortion, and then exactly minimized this for the mapping between two LGNs and an elliptical cortex. However, their result was obtained by a brute-force minimization of the cost function, without a particular biological mechanism in mind.

3 Monocular Deprivation

If one eye is occluded or sewn shut during the critical period for ocular dominance development in the cat or monkey, it is found that substantially more of the cells in layer IV of primary visual cortex can be driven by the normal eye as compared to the deprived eye. The anatomical correlate of this is that ocular dominance stripes receiving input from the normal eye expand at the expense of the stripes from the deprived eye: however, stripe periodicity remains the same (see e.g. for the cat [Shatz & Stryker 1978] and for the macaque [Hubel et al 1977]).

It is the matching term in the elastic net which determines the amount of "pull" each LGN unit exerts on the cortical sheet. In equation 1 each LGN unit exerts the same total pull. We modelled monocular deprivation by a procedure analogous to that used in other models (e.g. [Miller et al 1989]). The pull of all the units in one LGN was reduced by a fixed amount, corresponding to a decrease in competitive strength for that eye. This is most simply achieved by redefining the constant α so that it has a different value for each eye. The amount of deprivation, or "deprivation parameter", was defined to be the ratio of α for the deprived eye to that for the normal eye. The variation of stripe pattern with the size of this deprivation parameter is shown for the elastic net algorithm in figure 2. It can be seen that the deprived eye takes over less of the cortex than the normal eye: the deprived-eye stripes become thinner. However, the stripe periodicity remains the same as in the normal case. Note that we have only changed α, all other parameters remaining the same.

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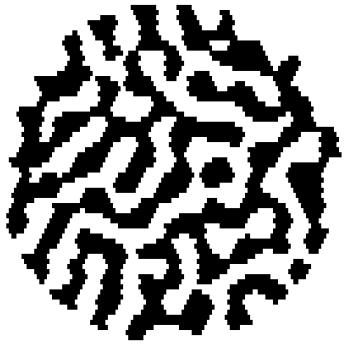
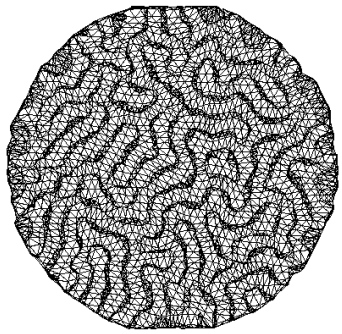
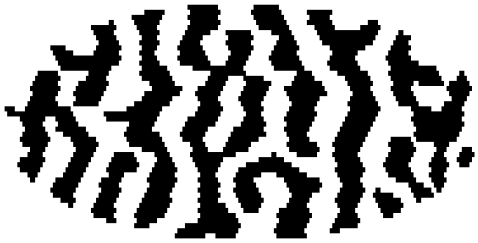
(a) (b)





(c) (d)



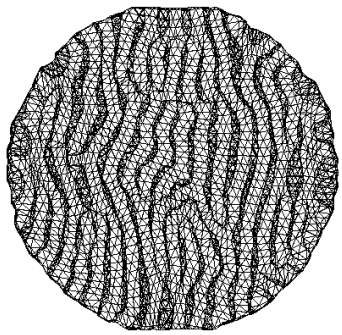


Figure 1: The effect of the shape of the cortex on overall stripe pattern. Each LGN was a unit disk of approximately 1750 units arranged in a hexagonal array. The disks were separated by a gap of 0.08. A small random component was added to each 3-D position to prevent any artefacts that might arise from complete regularity. The cortical sheet contained approximately 3500 units in a hexagonal array, bounded by either a circle (a, b), or an ellipse (c, d). Results are shown after 250 iterations: a slightly more efficient optimization procedure than steepest descent was used to reduce computation time (see e.g. [Durbin & Mitchison 1990, Goodhill 1991]). (a) and (c) show the ocularity of cortical units: each is coloured white or black depending on which LGN is closer. All units have become monocular. (b) and (d) show the positions of points in the cortical sheet, ignoring the ocularity dimension. The map in each case is topographic, apart from folding along the stripe boundaries. In the circular boundary case (a, b) there is no preferred stripe direction, whereas in the elliptical boundary case (c, d) stripes tend to be aligned parallel to the short axis. Other parameters: $\alpha = 0.2$, $\beta = 2.0$, initial value of $k = 0.2$, factor by which the annealing parameter k is reduced at each iteration $= 0.99$. Initial conditions were defined by assigning each cortical unit an arbitrary ocularity value, and a topographic position was chosen randomly from a uniform distribution within 0.5 (ie half the width of the LGN sheets) of its "ideal" location.

(a) (b)

Figure 2: Effects of monocular deprivation. For the "black" eye, $\alpha = 0.2$. (a) Deprivation parameter $= 0.75$. (b) Deprivation parameter $= 0.5$. All other parameters (including initial conditions) as in figure 1(c, d). Stripes representing the deprived eye become increasingly narrow as the size of the deprivation parameter is increased.

Bibliography

Dayan, P.S. (1993). Arbitrary elastic topologies and ocular dominance. *Neural Computation*, **5**, 392-401.

Durbin, R. & Mitchison, G. (1990). A dimension reduction framework for understanding cortical maps. *Nature*, **343**, 644-647.

Durbin, R. & Willshaw, D.J. (1987). An analogue approach to the travelling salesman problem using an elastic net method. *Nature*, **326**, 689-691.

Fraser, S.E. (1985). Cell interactions involved in neural patterning. In *Molecular Bases Of Neural Development*, eds. G.M. Edelman, W.E. Gall & W.M. Cowan, 481-507, Wiley, New York.

Goodhill, G.J. (1991). *Correlations, Competition and Optimality: Modelling the Development of Topography and Ocular Dominance.* PhD Thesis, University of Sussex.

Goodhill, G.J. (1993). Topography and ocular dominance: a model exploring positive correlations. *Biological Cybernetics*, **69**, 109-118.

Goodhill, G.J. & Willshaw, D.J. (1990). Application of the elastic net algorithm to the formation of ocular dominance stripes. *Network*, **1**, 41-59.

Hubel, D.H., Wiesel, T.N. & LeVay, S. (1977). Plasticity of ocular dominance columns in monkey striate cortex. *Phil. Trans. R. Soc. Lond. B*, **278**, 377-409.

Jones, D.G., Van Sluyters, R.C. & Murphy, K.M. (1991). A computational model for the overall pattern of ocular dominance. *J. Neurosci.*, **11**, 3794-3808.

LeVay, S., Connolly, M., Houde, J. & Van Essen, D.C. (1985). The complete pattern of ocular dominance stripes in the striate cortex and visual field of the macaque monkey. *Jou. Neurosci.*, **5**, 486-501.

Löwel, S. and Singer, W. (1993). Experience-dependent patterning of cortical connections in the visual system of cats. In: Elsner,N. and Heisenberg,M. (eds): Genes, Brain and Behavior. Proceedings of the 21st Göttingen Neurobiology Conference. Stuttgart-New York: Thieme. pp: in press.

Malsburg, C. von der (1979). Development of ocularity domains and growth behaviour of axon terminals. *Biological Cybernetics*, **32**, 49-62.

Miller, K.D., Keller, J.B. & Stryker, M.P. (1989). Ocular dominance column development: Analysis and simulation. *Science*, **245**, 605-615.

Obermayer, K., Blasdel, G.G. & Schulten, K. (1992). Statistical-mechanical analysis of self-organization and pattern formation during the development of visual maps. *Phys. Rev. A*, **45**, 7568-7589.

Shatz, C.J. & Stryker, M.P. (1978). Ocular dominance in layer IV of the cat's visual cortex and the effects of monocular deprivation. *Jou. Physiol.*, **281**, 267-283.

Swindale, N.V. (1980). A model for the formation of ocular dominance stripes. *Proc. R. Soc. Lond. B*, **208**, 243-264.

Willshaw, D.J. & Malsburg, C. von der (1979). A marker induction mechanism for the establishment of ordered neural mappings: its application to the retinotectal problem. *Phil. Trans. Roy. Soc. B*, **287**, 203-243.

Yuille, A.L., Kolodny, J.A. & Lee, C.W. (1991). Dimension reduction, generalized deformable models and the development of ocularity and orientation. *Harvard Robotics Laboratory Technical Report no. 91-3.*